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THE NODAL ANATOMY OF MYROTHAMNUS FLABELLIFOLIUS (MYROTHAMNACEAE): ANOTHER EXAMPLE OF A "SPLIT-LATERAL" CONDITION

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IN 1970, HOWARD SUGGESTED the "split-lateral" or "common gap" condition as another type of nodal anatomy worthy of recognition. In his review he reported that members of the Asteraceae, Caprifoliaceae, Chloranthaceae, Gentianaceae, Gesneriaceae, Rhizophoraceae, Rubiaceae, and Zygophyllaceae have "split-laterals." To his list I can add the Myrothamnaceae, a monotypic family often associated with the Hamamelidales, but also considered in connection with the Magnoliales.¹

MORPHOLOGICAL DESCRIPTION

The branches of the shrubby *Myrothamnus flabellifolius* show a clear differentiation into long and short shoots and bear decussately arranged leaves which exhibit a number of peculiarities.¹ The following characters are essential for an understanding of the vascularization pattern of the plant.

The "Unterblätter" (leaf bases) of each pair of opposite leaves are

fused (gamophyllous) and form a sheath which remains on the shoot after the "Oberblatt" (leaf blade) has abscised (see FIGURE 1, insert: the dotted line between "g" and "h" marks the position of the abscission zone). In short shoots, the "Unterblätter" remain rather small (ca. 1.5 mm.), are tightly packed, and overlap considerably — a single section through a short shoot may hit as many as three pairs of leaf bases (also see Puff, 1978, *fig. 4b*). In long shoots (FIGURE 1, insert) they appear much longer; a short distance from a node downward, however, they fuse with the stem, making a distinction between leaf and stem impossible (see FIGURE 1, sections a-c). They bear two kinds of appendages: four lateral ridges (FIGURE 1, insert: R) which run down the whole length of the internode and terminate as "stipules" or stipule-like appendages (FIG-URE 1, insert: S) just below the abscission zone; and adaxially, between leaf base and stem, the "vaginal" or "median" lobes (FIGURE 1, insert: V),

which often envelop newly developed lateral shoots (FIGURE 1, insert: L).

VASCULARIZATION PATTERN

For the sake of greater clarity, consecutive sections cut through a long shoot are presented in FIGURES 1 and $2.^2$

¹For a recent compilation of our knowledge of *Myrothamnus*, see Puff (1978). ²The vascularization pattern of short shoots is not different, but is much more difficult to interpret because of the short internodes and the overlapping, tightly packed "Unterblätter."

1978] PUFF, MYROTHAMNUS FLABILLIFOLIUS

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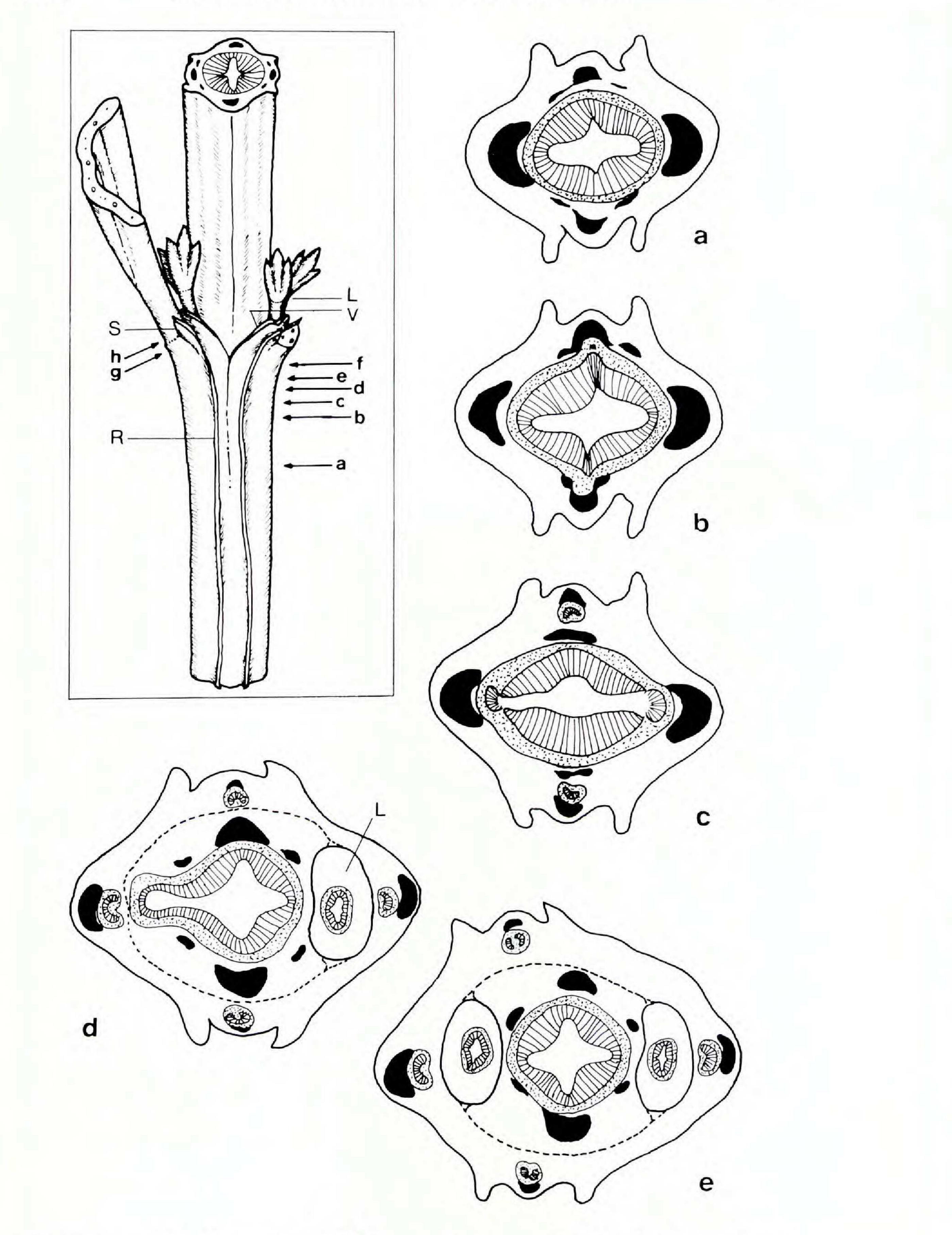


FIGURE 1. Myrothamnus flabellifolius. a-e: camera lucida drawings of sections through a long shoot. Insert: portion of a long shoot; arrows indicate where sections a-e and f-h (FIGURE 2) were cut. Black areas: sclerenchymatic tissue; hatched areas: xylem; dotted areas: phloem.

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Sections a-c show the characteristic four ridges that, starting at the abscission zone, run down the whole length of the internode; they are not vascularized. At the level of sections a, b, and c, no differentiation can be made between "leaf" and "stem" in spite of the presence of these ridges. Massive sclerenchyma strands run through the cortex in the median; two somewhat smaller ones (each of them accompanied by a small band on either side) are in the area between two adjacent ridges (section a).

At a somewhat higher level (section b), two lateral traces depart from the vascular cylinder, and slightly above (section c), the two median bundles branch out. At this point, the gaps of the laterals are closed again, and the sclerenchyma has formed a sickle-shaped sheath around them towards the outside, as well as a small strand between the bundles and the stele.

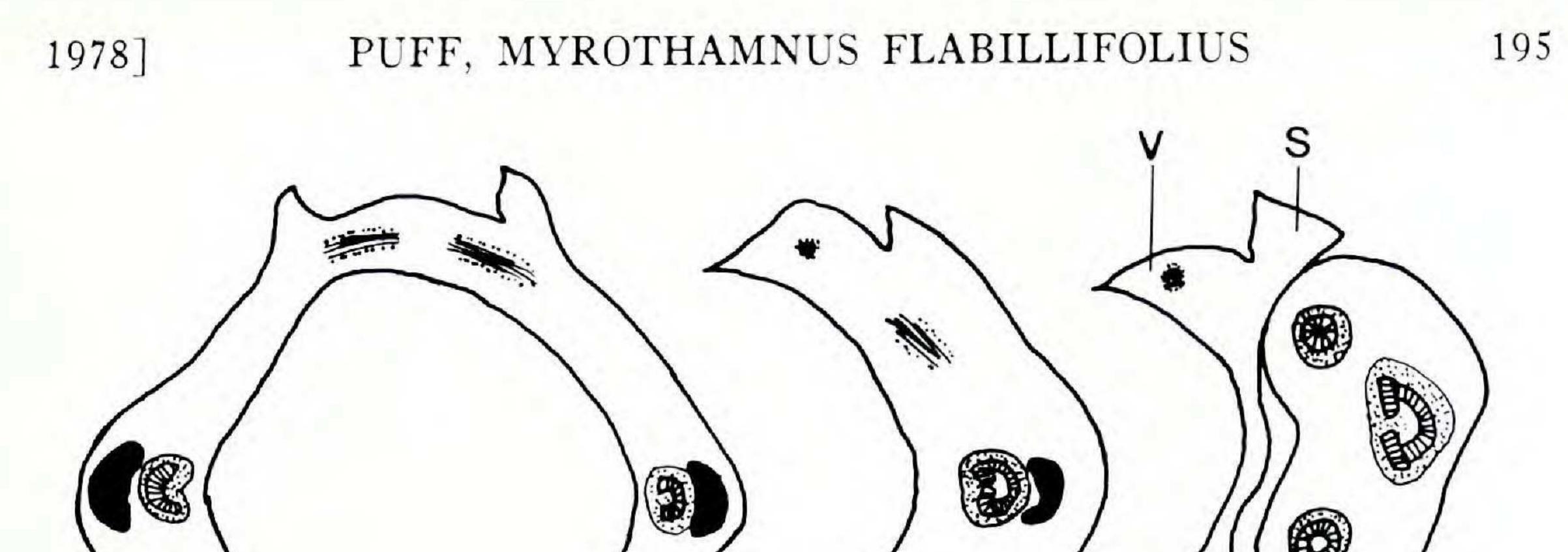
As we further approach the node, the vascular cylinders supplying the lateral shoots (L) can be seen departing from the stele (section d; not cut exactly at a right angle to the stem). It should be mentioned that at this stage the gamophyllous "Unterblätter" and the stem now have become two distinct units (sections d and e: dotted line). The leaf bases remain fused, although they also envelop the newly produced lateral shoots. The amount of sclerenchymatic tissue has increased in the stem: now there are two massive lateral strands plus four smaller ones. A little higher (section e), the four traces of the "Unterblätter" can still be seen ascending in a vertical direction. There is, however, a first indication that the two lateral traces are beginning to split: the bundles which appeared as semicircles in sections c and d are starting to separate into two units. In section f (only fused leaf bases shown), finally, the two lateral bundles fork, with a portion moving toward each of the opposite median traces. Section g, cut slightly below the abscission layer, shows the lateral traces still passing through the leaf base toward the median bundle. They have forked again, and two small traces have entered the sides of the "vaginal lobe" (V). Slightly higher, section h cuts the base of the leaf blade (with the large median and the two circular lateral bundles), and the "vaginal lobe" (with two small lateral traces) and "stipules" (no vascularization), neither of which is any longer connected with the blade.

Within the leaf blade, the traces split up further. Normally, however, only the median bundles fork once or twice, while the lateral traces often

remain unbranched (also see Grundell, 1933, fig. 6).

DISCUSSION

The Myrothamnaceae so far are the ninth family of dicotyledons with "split-laterals." It, however, appears to be the only family in which "split-laterals" are a family characteristic: preliminary investigations of herbarium material of Myrothamnus moschatus Baillon, the only other species of the genus (or of the family), yielded a vascularization pattern



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FIGURE 2. Myrothamnus flabellifolius: camera lucida drawings of sections through leaf bases. Black areas: sclerenchymatic tissue; hatched areas: xylem; dotted areas: phloem.

very similar to that of M. flabellifolius. More material, however, is needed to verify this.

Myrothamnus flabellifolius, like the other plants known to have splitlateral traces, has opposite (decussate) leaves and "stipules" or stipulelike processes³ (for exceptions, see Howard, 1970). Unusual, and so far not known in plants with split-lateral bundles, however, are the gamophyllous "Unterblätter" of M. flabellifolius, which completely envelop the stem (and the bases of newly produced lateral shoots). In M. flabellifolius, the lateral bundles fork within the leaf (i.e., "Unterblatt"), and not, as in other plants with "split-laterals," in the stem (cortex): only after ascending vertically in the leaf base for a distance do they fork, pass around about a quarter of the "Unterblatt," and eventually join the median trace laterally (a "shift" of the "split-lateral" from the stem region to the leaf). As "stem" and "leaf," however, must developmentally and morphologically be considered a continuous system (see Howard, 1974), this peculiarity of M. flabellifolius appears to be of little significance.

PLANT MATERIAL EXAMINED

Southwest Africa (Namibia): Ameib farm near Usakos, on path to Phillips Cave, Puff 760714-1/2; Gamsberg pass, Puff 760717-1/1 and -2/1. South Africa. N. NATAL: Ngotoshe Dist., Ngome, near sawmill, Puff 760610-5/1. TRANSVAAL: Bosmanskop area near Badplaas, Puff 770103-7/3; Wolkberg area near Haenertsburg, Puff 770108-5/2.

Swaziland: Mdzimba Hills near Mbabane, Puff 770119-1/1; Lebombo Mts., Blue Jay Ranch, near Mozambique border, Puff 770123-3/4.

³ In addition, it has "vaginal lobes." The true morphological nature of both "stipules" and "vaginal lobes" has yet to be clarified. An ontogenetic study could prove to be useful: according to Weberling (1975), true stipules always develop early and distinctly proleptically, whereas other appendages ("sheath lobes" of Weberling) develop at a later stage.

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All specimens are deposited at the herbarium of the Institute of Botany, University of Vienna (WU).

Sections were cut freehand with a razorblade and stained in phloroglucinol and hydrochloric acid.

LITERATURE CITED

GRUNDELL, R. 1933. Zur Anatomie von Myrothamnus flabellifolia Welw. Symb.

- Bot. Upsal. 1(2): 1-17.
- HOWARD, R. A. 1970. Some observations on the nodes of woody plants with special reference to the problem of the "split-lateral" versus the "common gap." Pp. 195-214 in N. K. B. ROBSON, D. F. CUTLER, and M. GREGORY, eds., New research in plant anatomy. Jour. Linn. Soc. Bot. 63, Suppl. 1. Academic Press, London and New York.
- ——. 1974. The stem-node-leaf continuum of the Dicotyledoneae. Jour. Arnold Arb. 55: 125–181.
- PUFF, C. 1978. Zur Biologie von Myrothamnus flabellifolius Welw. (Myrothamnaceae). Dinteria (in press).
- WEBERLING, F. 1975. Über die Beziehungen zwischen Scheidenlappen und Stipeln. Bot. Jahrb. Syst. 96: 471-496.
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